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A CONTROLLED HYBRID BETWEEN SITANION HYSTRIX AND AGROPYRON TRACHYCAULUM

W. S. Boyle

Students of evolution have become increasingly aware of the extensive hybridization that exists between genera and species in the grass family, particularly the tribe Hordeae. Probably no other family in the plant kingdom is destined to undergo such a fundamental revision of concepts of genetic relationships among genera as is occurring gradually in the Gramineae.

The present paper reports the meiotic chromosome behavior, fertility, and comparative morphology of a controlled hybrid between *Sitanion hystrix* (Nutt.) J. G. Smith and *Agropyron trachycaulum* (Link) Malte.

Materials and Methods

Specimens of *A. trachycaulum* growing in fields near Logan, Utah, and those of *Sitanion hystrix* from Mantua, Utah, were transplanted to a field nursery in 1954. The crosses were made the following year.

Forty florets involving several spikes of *S. hystrix* were hand-emasculated in June. Mature culms of *Agropyron trachycaulum* were placed in bottles of water and the bottles taped to stakes driven in the ground beside the culms of *Sitanion hystrix*. Each culm of *S. hystrix*, with its adjacent pollinators, was then covered with Kraft paper sacks.

Two seeds were harvested in early August and planted later that same month in the greenhouse. The plants grew vigorously and a few spikes were produced the following year. One plant proved simply to be a selfed

S. hystrix, but the other was indeed the hybrid. This was divided and repotted.

From 1959–1960 the plants grew well in the greenhouse but the production of flowering culms was sporadic. It was concluded that the high summer temperatures in the greenhouse interfered with normal anthesis; therefore the five clones were transplanted to the field nursery. In the field, they grew very well and flowered normally (fig. 2). The importance of field observations was emphasized by the contrast between plants grown in the greenhouse and the same plants grown in the field nursery. In addition to much greater height, the plants grown in the field possessed inflorescences larger in all respects than those of plants grown in the greenhouse.

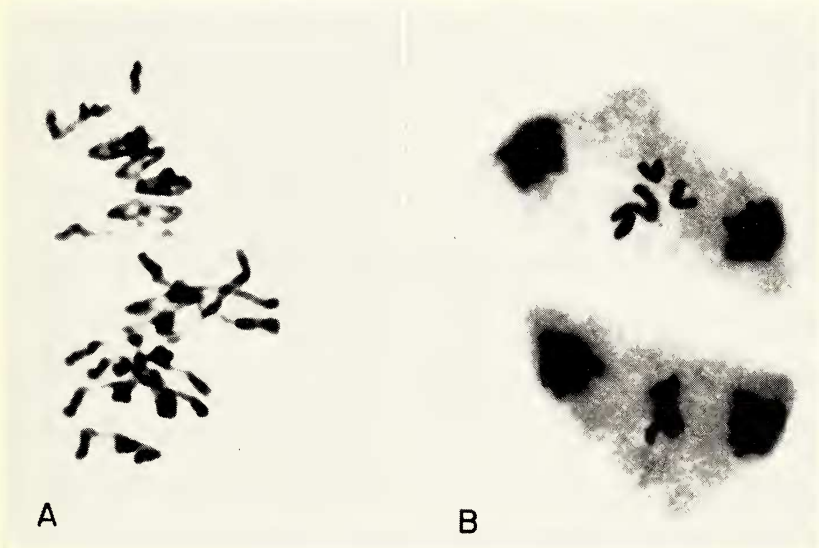

Fig. 1. Meiosis in the hybrid: A, metaphase I, pollen mother cell, 12 II, 1 IV (× 1100); B, telophase II, pollen mother cell, lagging chromosomes (× 1315).

Numerous spikes were removed in the boot stage and fixed in Newcomer's solution (1953). Observations and photographs were taken from acetocarmine smears in temporary mounts.

Meiotic Chromosome Behavior

Metaphase I. Chromosome associations in the 204 pollen mother cells that were interpreted are summarized in Table 1. Although 24 different types of chromosome association were observed, approximately 75 per cent fell into the following categories: 14 II (23.5 per cent); 12 II, 1 IV (23.5 per cent); 13 II, 2 I (14.7 per cent); 11 II, 1 IV, 2 I (12.7 per cent). Figure 1A is representative. Bivalents were present in all cells and averaged 12.2 per cell. Univalents averaged 1.13 per cell with a range of 0–6. Over half the cells possessed one or more quadrivalents, with an

average of 0.6 per cell and a range of 0–3. Three trivalents and one hexavalent were observed.

Telophase I, II. Approximately a third of the 847 cells examined at telophase I contained one or more lagging chromosomes (Table 2). They averaged 0.6 per cell and had a range of 0–6. Nearly half of the 1756 cells examined at telophase II contained one or more lagging chromosomes, with an average of 0.78 and a range of 0–7 (fig. 1B).

Fig. 2. The hybrid in the field ($\times$ 1/16). Fig. 3. Spikes: A, *Sitanion hystrix;* B, the hybrid; C, *Agropyron trachycaulum* ($\times$ 1/4).

Tetrads. Micronuclei averaged 0.37 per cell in the 2361 pollen grains examined at the tetrad stage. This is equivalent to 1.43 micronuclei per pollen mother cell. Approximately 70 per cent were without micronuclei. The maximum number of micronuclei in any one pollen grain was 3.

Pollen. The pollen was almost entirely abortive. Of the 9064 mature pollen grains examined, only 3 appeared to be fertile.

Fertility

In a careful search of approximately 2500 florets, not a single seed was found. The hybrid is completely sterile.

Comparative Morphology

The parental species are both highly variable, as the long synonomy lists suggest. However, obvious general differences exist between the two parents with respect to the morphology of the inflorescence. Except in size relationships, the hybrid is approximately intermediate between the two parents (figs. 3, 4).

Table 1. Chromosome Association at Metaphase I.

	I	II	III	IV	VI	Number cells
		14				47
		12		1		47
	2	13				30
	2	11		1		26
	4	12				12
		10		2		11
	4	10		1		7
		13		1		5
	2	9		2		3
	3	11		1		2
	1	13	1			1
	2	12				1
	6	11				1
	5	10	1			1
		12		2		1
	3	10	1			1
	4	9		1		1
	2	7		3		1
		11			1	1
	4	11				1
		11		1		1
	3	10		1		1
		13				1
	1	12	1			1
Average per cell	1.13	12.2	0.19	0.60	0.004	204 Total No.

In *Agropyron trachycaulum* the spikelets occur singly at the nodes, the rachis does not disarticulate, the glumes are very broad, and both glumes and lemmas are awnless. In *Sitanion hystrix* the spikelets usually occur in pairs, the rachis readily disarticulates at maturity, the glumes are very narrow, and both glumes and lemmas terminate in long, frequently twisted awns.

In the hybrid the spikelets occur singly at the nodes, the rachis tardily disarticulates at maturity, the glumes are moderately wide, and both glumes and lemmas have fairly short (1½ cm.), diverging awns. The hybrid is a vigorous, tall bunchgrass apparently possessing considerable hybrid vigor.

Discussion

The average number of univalents per pollen mother cell approximates the average number of micronuclei per pollen mother cell. The univalents would be expected to lag at first and second telophase and doubtless are the source of the micronuclei. The average number of laggards reported per cell at telophase I and II, however, was much lower than expected. A plausible explanation for this discrepancy could be our overly conserva-

tive tendency in identifying laggards. Only chromosomes in the center of the plates were stipulated as laggards (fig. 1B). Very likely other chromosomes that approached the poles nevertheless failed to be included in the new nucleus and remained outside to form micronuclei.

The absence of quadrivalents in cytological studies of the parents tends to suggest that both are allotetraploids, and that the pairing in the hybrid is allosyndetic. Therefore these two species may have more or less homologous genomes. On the other hand, Wagenaar (1959) has convincingly demonstrated autosyndesis among *Hordeum* chromosomes in a hybrid between *H. jubatum* L. and *Secale cereale* L. No quadrivalents were observed in the *Hordeum* parent. Dewey (1961) has conclusively demonstrated autosyndesis among chromosomes of *Agropyron repens* (L.) Beauv. and *A. desertorum* (Fisch.) Schult. in a hybrid between them. Stebbins and Pun (1953) similarly demonstrated that chromosomes of *A. intermedium* (Host.) Beauv. paired autosyndetically in a hybrid between that species and *S. cereale*.

Table 2. Frequency of Lagging Chromosomes at Telophase I and Telophase II.

	Average number of laggards per cell	Percent with one or more laggards	Number of cells
Telophase I	0.60	34.1	847
Telophase II	0.78	48.5	1756

Since the writer cannot distinguish between the parental chromosomes in the hybrid, the precise nature of the pairing obviously cannot be inferred with confidence. The high frequency of quadrivalents, however, permits some speculation on homologies between these species. Over 50 per cent of the metaphase I plates possessed one or more quadrivalents. It is most unlikely that reciprocal translocation is responsible for any substantial percentage of these quadrivalents since they are absent in approximately half the cells and occur in variable numbers of the cells that do contain them. Even if it is conceded that the bivalent pairing may be exclusively autosyndetic, which is by no means established, the high number of quadrivalents suggests that important homologies exist between *Agropyron trachycaulum* and *Sitanion hystrix*. The degree of homology cannot be accurately assessed at present, but these two species unquestionably are much more closely related than their present taxonomic status indicates.

Stebbins *et al.* (1946) reported a controlled hybrid between *Sitanion hystrix* and a species of *Agropyron* ("San Benito") believed to be most closely related to *A. parishii* Scribn. & Smith but originally identified as *A. trachycaulum*. The bivalent frequency (12.7 per cell average) closely approximates that of the hybrid reported in this paper. The frequency of univalents, laggards, and micronuclei in Stebbins' hybrid, however, was much higher and the quadrivalent frequency was much lower than those

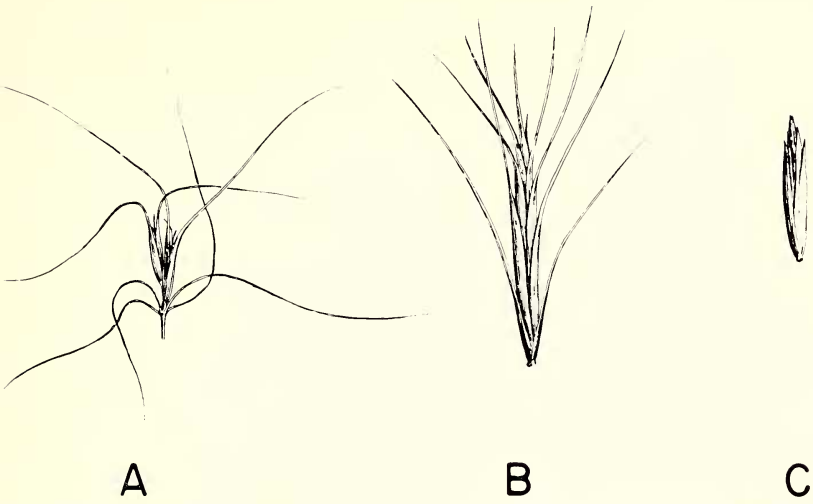

FIG. 4. Spikelets: A, *Sitanion hystrix*; B, the hybrid; C, *Agropyron trachycaulum* (× 2).

found in the hybrid of this study. In the Stebbins' contribution the authors suggested that *A. saundersii* (Vasey) Hitchc. is probably an F_1 hybrid between *A. trachycaulum* and *Sitanion hystrix*. The present study lends some, but not complete, support to this proposition. The type specimen of *Agropyron saundersii* has considerably longer awns and shorter spikes than the controlled hybrid produced in the present study. Furthermore, in the type specimen of *A. saundersii* the spikelets are frequently paired, in contrast to the single spikelets of the hybrid of the present study. Professor Arthur H. Holmgren has made the very plausible suggestion (oral commun.) that *Sitanion longifolium* J. G. Smith has served as one parent of *Agropyron saundersii*. This species (sometimes referred to *Sitanion hystrix*) has large, coarse spikes with long, straight awns, and could well account for the differences observed between *A. saundersii* and the hybrid of the present study. *Sitanion longifolium* is known to be present in the general region where the type of *Agropyron saundersii* was collected.

SUMMARY

A controlled hybrid between *Sitanion hystrix* and *Agropyron trachycaulum* is reported. Although 24 different types of chromosome associations were observed at metaphase I in 204 interpreted pollen mother cells, 75 per cent fell into the following four categories: 14 II; 12 II, 1 IV; 13 II, 2 I; 11 II, 1 IV, 2 I. Bivalents were present in all cells and averaged 12.2 per cell. Over half of the pollen mother cells contained one or more quadrivalents. Univalents averaged 1.13 per cell. Lagging chromosomes averaged 0.60 per cell at telophase I and 0.78 at telophase II.

Micronuclei averaged 1.43 per pollen mother cell. The hybrid is completely sterile.

Although it was not possible to distinguish between autosyndetic and allosyndetic pairing, the high frequency of quadrivalents in the hybrid suggests that important homologies exist between the parental species.

The hybrid is morphologically intermediate between the two parents except for size relationships. Some support is given to the suggestion that *Agropyron saundersii* had a similar origin.

Acknowledgment

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Utah State University
Logan, Utah

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CYTOTAXONOMIC OBSERVATIONS ON MENTZELIA, SECT. BARTONIA (LOASACEAE)

Henry J. Thompson[1]

A previous investigation (Thompson & Lewis, 1955) stated that information about chromosome numbers in *Mentzelia* would be of great value in the formation of evolutionary and taxonomic concepts in the genus. Section *Trachyphytum*, represented by twenty populations of ten species, was shown to be a polyploid complex on the base x=9, with diploids (n=9), tetraploids (n=18), hexaploids (n=27), and octaploids (n=36). On the other hand, polyploids were not found in section *Bartonia*, although only two species were examined cytologically: *Mentzelia multi-*

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